

Climatic forcing of evolution in Amazonia during the Cenozoic: On the refuge theory of biotic differentiation *

by

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Abstract

Climatic-vegetational fluctuations due to astronomical Milankovitch cycles caused global changes in the distribution of tropical forests and nonforest vegetation during the Cenozoic (Tertiary-Quaternary) and before. Forest and nonforest biomes on the continents changed continuously in distribution during the geological past, breaking up into isolated blocks and again expanding and coalescing under the varying dry to humid climatic conditions. However, plant and animal communities disrupted and species changed their distributions individually during the various climatic phases. Field data indicating vegetational changes in Amazonia exist for the Quaternary.

The refuge theory postulates that extensive patches of humid rainforests persisted during dry periods of the Tertiary and Quaternary, especially near areas of surface relief in peripheral portions of Amazonia, where many extant species and subspecies of plants and animals probably originated. The humid 'refugia' may have been separated by various types of savanna and dry forests as well as other intermediate vegetation types of seasonally dry climates. The number and size of refugia during different dry periods remain unknown. Biogeographic evidence for the former existence of forest refugia include areas of endemism and sharply defined contact zones between species and subspecies of Amazonian forest birds and other animals which represent zones of conspicuous biogeographic discontinuity in a continuous forest environment.

Alternative models of barrier formation in Amazonia leading to allopatric speciation include the river hypothesis, river-refuge hypothesis, canopy-density hypothesis, disturbance-vicariance hypothesis, museum hypothesis and various paleogeography hypotheses, some aspects of which may be applicable to certain periods in the evolution of the biota.

Keywords: Refugia, Amazonia, paleoecology, geographic speciation, Milankovitch cycles.

*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

Flutuações climáticas e de vegetação causadas pelos ciclos astronômicos de Milankovitch provocaram mudanças globais na distribuição de florestas tropicais e demais vegetações não-florestais antes e durante o Cenozóico (Terciário-Quartenário). Em seu passado geológico os biomas continentais de florestas e vegetações não-florestais mudaram continuamente em sua distribuição, formando blocos isolados, expandindo e se juntando novamente perante condições climáticas alternando entre secas e húmidas. Mas durante as diversas fases climáticas as comunidades de plantas e animais se separaram e as espécies mudaram suas distribuições individuais. Dados de campo indicando mudanças na vegetação da Amazônia existem para o Quartenário.

A teoria do refúgio postula a persistência de áreas extensas de florestas tropicais húmidas durante os períodos secos do Terciário e Quartenário, especialmente aquelas localizadas perto de relevos de superfícies nas periferias da Amazônia. Estas áreas provavelmente são a origem de muitas espécies e sub-espécies de plantas e animais existentes hoje em dia. Existe a possibilidade destes 'refúgios' húmidos terem sido separados por vários tipos de savana e florestas secas como também por outros tipos de vegetação intermediária. A quantidade e o tamanho dos refúgio durante os diferentes períodos de seca continuam desconhecidos. Evidências biogeográficas da existência de refúgios florestais anteriores incluem áreas de endemismo e zonas de contato entre espécies e sub-espécies de pássaros e outros animais da floresta amazônica rigorosamente definidas. Estas áreas representam zonas biogeográficas inegavelmente descontínuas dentro de um ambiente de florestas contínuo. Existem modelos alternativos para a formação de barreiras na Amazônia que possibilitam o surgimento de espécies alopátricas: a hipótese do rio, a hipótese do refúgio do rio, a hipótese densidade-copa, a hipótese da perturbação-vicária, a hipótese do museu e várias hipóteses paleogeográficas, das quais alguns aspectos poderiam ser aplicáveis a certos períodos na evolução do biota.

Introduction

Extensive data from the Old World tropics document the occurrence of numerous drought periods in these regions during the past 60 million years (Tertiary and Quaternary). Africa and Australia experienced a continuation of wet-dry climatic cycles and, during the last 2.8 million years, were subjected to periodic cold-dry periods corresponding to the succession of glacial stages of the Plio-Pleistocene. Lake levels were strongly reduced across tropical Africa during these climatic phases. However, changes probably did not occur homogeneously across the Continents. In a global review of the origin and evolution of tropical rainforests MORLEY (2000: XIII, 280) emphasized that "their immense diversity is due not to a long, unchanging history, with stable climatic conditions over millions of years, but to the ability of opportunistic plants to survive through periods of climate change and geological upheaval, to expand their distributions when changing climates permit, to retreat to favourable refuges when climates were unfavourable. ... Diversification of tropical rain forest floras has continued through a major part of the Tertiary, as a result of their successive expansion and retraction and fragmentation by physical barriers, and is not exclusively a Quaternary phenomenon". The recurrence of dry climatic events and their associated effects on the Old World floras and faunas during the Cenozoic (Tertiary and Quaternary) have been widely discussed as the primary forcing agent behind evolutionary responses of the biota (see various chapters in GOLDBLATT (1993) and VRBA et al. (1995)). What was the situation in South America, particularly in Amazonia, during these geological periods? Did its climatic history follow the global pattern? The purpose of this contribution is to

summarize and discuss the current stage of our knowledge of the climatic-vegetational history of Amazonia and its relevance for the evolution of the Neotropical forest floras and faunas.

Most species of plants and animals probably originated from populations that developed genetic-reproductive isolating mechanisms from their parent species during one or more periods of geographical separation (geographical or allopatric speciation; MAYR 1942, 1963; AVISE 2000). Sympatric speciation within the range of parent species without geographic separation was very rare (TREGENZA & BUTLIN 1999). Therefore the question arises as to which barriers fragmented the ranges of ancestral species in Amazonia repeatedly to permit new species to develop. Through pervasive intermediate disturbance of the forests caused by erosion and lateral migration of rivers across their floodplains and by gap formations (storms and treefalls) a complex mosaic of mature forest, successions and gaps is developed which helps explain the maintenance of the high Amazonian species diversity. However, these disturbances provide insufficient separation for plant and animal populations to differentiate into new sub-species and species.

The effect of dry climatic periods in Amazonia during the Quaternary

The resolution of the geological record pertaining to the Tertiary and older periods worldwide is not finegrained and detailed enough to document the global effect of the astronomical Milankovitch cycles* except in certain favorable local situations (HERBERT & FISCHER 1986; OLSEN 1986; BARTLEIN & PRENTICE 1989; BENNETT 1997). These cycles at the 20 thousand to 100 thousand year time-scales are (1) precession cycles (ca 20,000 years) due to the changing distance between the earth and the sun, (2) obliquity cycles (ca 40,000 years) due to the increasing and decreasing tilt of the equator on earth's orbit around the sun, and (3) eccentricity cycles (ca 100,000 years) due to the changing shape of the earth's orbit around the sun. Their main effect was an alternation of relatively dry and more humid climatic periods on the continents with corresponding changes in the distribution of forest and nonforest vegetation. These geologically rather short-term (high-frequency) oscillations were superimposed on a gradual cooling trend of the earth's climate since the early Cenozoic. The latitudinal thermal gradient steepened during the course of the Tertiary, when annual average temperatures increased in the tropics and the summer temperatures decreased in higher latitudes. During the Quaternary, the relatively dry (glacial) periods were cooler also in the tropics and the humid interglacial periods were relatively warm.

The biotic effect of such climatic changes during the Quaternary and the Tertiary probably was that communities disrupted and species changed their distributions individually. Nevertheless, there have always been closed vegetation types (forests) and open types with their respective animal communities during the various climatic phases, although their species composition changed to some degree. Because of these communi-

*MILUTIN MILANKOVITCH (1879-1958) was a Professor of Theoretical Physics and Celestial Mechanics at Belgrade University who analyzed, during the early 1930s, the three pacemakers of global climatic fluctuations during most or all of the geological history of the earth.

ty changes we do not speak of changes of plant 'formations'.

Although the data base is still sparse, much information on the effect of dry climates (not necessarily 'arid' climates) in Amazonia during the late Quaternary has become available in recent years (Fig. 1), however, the exact dating and the correlation of geological records in different regions remain open in many cases. What is important to establish at this stage is the general fact that dry climatic phases and corresponding shrinkage of humid rainforest definitely occurred over some parts of Amazonia. For this purpose, even undated evidence of dryness in the past is 'data' that should not be dismissed. We do not consider the results mentioned below as proof for the occurrence of Amazon-wide dry climatic phases during the Quaternary, but they do indicate climatic changes at least on a local and fairly regional scale. Of course, extensive areas of rainforest (which itself is very ancient) always existed in Amazonia. BURNHAM & GRAHAM (1999) and THOMAS (2000) discussed the evidence for climatic dryness in Amazonia in their excellent reviews of Quaternary environmental changes in humid tropical environments of the Neotropical Region and the world, respectively.

Large inactive dune fields have been discovered in northcentral Amazonia; this area, the 'Pantanal do Norte', covers an area of several thousand square kilometers between the rivers Branco and Negro (SANTOS et al. 1993; see Fig. 1, No. 1) and today is covered by the rather open vegetation that is locally termed Amazonian caatinga. The paleoclimatic relevance of these sand fields may, however, be limited if, upon re-examination, they turn out to be podsol sands (widespread in the Negro river system). Numerous smaller aeolian sand fields exist further north around Boa Vista (CARNEIRO FILHO & ZINCK 1994) and in central Amazonia between Manaus and the Atlantic Ocean. Their caatinga-like vegetation is termed campina (ANDERSON 1981) which also covers patches of uplifted river beds near Manaus (these, of course, have little to do with relatively dry climates). This vegetation is quite different from that of the savannas. It is the isolated savannas over clay soils that show that savanna plants have been distributed widely over the Amazon; for example the savannas around Santarém and the Savanna da Amelia on the south bank of the Rio Negro above Manaus. IRIONDO & LATRUBESSE (1994) have offered evidence for a dry Late Glacial climate in the central portion of lower Amazonia and commented on the reduced discharges of the rivers in this area and highly seasonal climatic conditions with enhanced Trade Winds. The latter authors stated that only second-order changes in the regional climatic dynamics are needed for the occurrence of a dry climatic phase in this region (Fig. 1, No. 2). In this same area, west of Santarém (near Óbidos) TRICART (1974: 146) observed "a highly dissected area, in spite of the dense forest cover. ... The slopes are very steep and the ridges very narrow. Such a dissection cannot develop under a dense forest cover. It implies sparse vegetation, more or less of the savanna type". He concluded later: "Central Amazonia has suffered the effects of dry periods when it ceased to be covered by the present type of rainforest Dense and sharp dissection of the ridges ... developed during the last period of low sea level, i.e. the last stage of the Würm (Wisconsin) glaciation. During this period, it is highly probable that central Amazonia was not covered by the present phytostabilising rainforest, but by drier types of vegetation under which runoff was able to produce slope dissection" (TRICART 1985: 197, 201). Humid conditions and gallery forests probably persisted along portions of the Amazon River itself and its major tributaries much as it does today in the savanna regions of South America and so this cannot be taken as evidence against a regionally dry climate

(MÜLLER et al. 1995). The importance of these forest corridors was emphasized by PRANCE (1982a).

The rainforest at Pitinga, ca. 250 kilometers north of Manaus, is underlain by layers of coarse and extremely poorly sorted sediments which must have been deposited under dry climatic conditions of the recent geological past when dense rainforests were absent from much of this region (VEIGA et al. 1988; Fig. 1, No. 3). The same interpretation applies to the sediments deposited in portions of southcentral Brazilian Amazonia in the regions of the rivers Xingú, upper and middle Tapajós and of northern Rondônia (VEIGA et al. 1988, 1991; BETTENCOURT et al. 1988). Coarse debris also accumulated in surface depressions in the middle Rio Tapajós region (Fig. 1, No. 4) and extensive sand layers covered the lowlands around Serra do Cachimbo (Fig. 1, No. 5) during a period of strong erosion when the late Pleistocene climate was dry and dense rainforest vegetation had largely disappeared from these regions (BIBUS 1983). In several complex soil profiles the latter author observed discordant layers indicative of climatic changes accompanied by strong morphodynamic activity. In southern Amazonia hills consisting of fresh (!) granite occur under rainforest cover which situation can only be explained by intervening periods of erosion, when the forest cover was more open or had disappeared completely. An extensive erosional phase occurred in the Rio Tapajós region during the late Pleistocene when open vegetation covered this portion of Amazonia. BIBUS (l.c.) also pointed out that the Pleistocene terraces in lower Amazonia contain thick layers of coarse sediments which indicate very different erosional conditions in lower Amazonia during the periods of deposition than those that exist in this region at the present time. Geomorphological observations on stone lines and stratified soils in Rondônia (EMMERICH 1988) around Porto Velho and phytogeographical studies near Humaitá (GOTTSBERGER & MORAWETZ 1986) also indicate dry climates and the periodic existence of open vegetation in this portion of southern Amazonia during the Plio-Pleistocene (Fig. 1, No. 6-7). Between 9,000 and 3,000 years BP, savanna vegetation expanded at the expense of forest in the area of Humaitá and Porto Velho (FREITAS et al. 2001). Palynological work of VAN DER HAMMEN & ABSY (1994) had also indicated the existence of savanna vegetation in this forest region to the southeast of Porto Velho during the Last Glacial Maximum. MAYLE et al. (2000) documented vegetational changes near the southern edge of the Amazonian forest region.

Throughout the Acre Subbasin in western Brazil (upper Rio Purús and lower Rio Acre), gypsum and aragonite precipitates associated with finegrained sediments indicate the desiccation of an extensive fluvial-lacustrine system due to dry climatic conditions about 53,000 years ago (KRONBERG et al. 1991; see Fig. 1, No. 8)**. In addition, paleontological studies of fossil mammals from the latter regions (and along the Rio Napo in eastern Ecuador) indicate that a vegetation consisting of wooded savannas and gallery forests was widespread in upper Amazonia during the late Pleistocene before dense rainforests again covered this region (RANCY 1991; WEBB & RANCY 1996; see Fig. 1, No. 9). Late Pleistocene faunal remains from the Juruá River floodplain

** RÄSÄNEN et al. (1995) treated sedimentary strata exposed in the upper Purús-Acre region as of late Miocene age. Additional studies are needed to verify the Quaternary age of the strata sampled by KRONBERG et al. (l.c.) and the Tertiary age of the sediments studied by RÄSÄNEN et al. (l.c.) in this area.

sediments in SW Amazonia also indicate open country before 40,000 BP (LATRUBESSE & RANCY 1998). MARSHALL (1979), WEBB (1991) and WEBB & RANCY (1996) discussed evidence of dry climatic periods in the lowlands of Central and South America during the past several million years which permitted an exchange of northern and southern mammal faunas through corridors of open vegetation across Amazonia.

Fossil pollen data from the middle Rio Caquetá region in southeastern Colombia indicated that, during drier periods of the Pleniglacial, savanna-caatinga type vegetation could develop there or extend somewhat locally (Fig. 1, No. 10). The relatively small plateaux of the Serra dos Carajás, State of Pará, are covered today with open canga (ironstone) vegetation because of edaphic conditions and are surrounded on all sides by dense rainforests covering the slopes and intervening lowlands (see, SECCO & MESQUITA 1983 and Fig. 1, No. 11). Geological studies and analyses of fossil pollen revealed four periods of rainforest regression from this general region during the last 60,000 years (ABSY et al. 1991; SIFEDDINE et al. 1994; see, however, critical comments by COLINVAUX et al. 2000: 157).

During the glacial periods, when global sea level was up to 120 meters lower than at present, the regional groundwater table was lowered and the Amazon River and the lower portions of its tributaries flowed in comparatively narrow 'canyons'. Combined with a regionally drier climate than today, this probably had a severe effect on the vegetation because of a reduced availability of water. This, in turn, led to widespread changes in forest composition and forest shrinkage throughout much of middle and lower Amazonia, where the precipitation is mostly convectional and where a pronounced dry season presently occurs (SALATI 1985). Similarly, BURNHAM & GRAHAM (1999: 569) stated: "Considering that much of the Amazon Basin is near sea level, a lowering of sea level by ca. 121 ± 5 m at glacial maximum must have had some drying effect on vegetation through fluctuations in water table." The vast fields of fossil dunes in the Llanos region of eastern Colombia-Venezuela to the northwest of Amazonia, indicate that this portion of South America became desert-like during certain periods of the Quaternary. CLAPPERTON (1993a) stated that: "The convergence of evidence continent-wide supports the concept of drier conditions and less closed-forest cover at the glacial maximum." The ice core records from the Peruvian Andes document a 200-fold increase in atmospheric dust during the Last Glacial Stage possibly because forest cover in the nearby Amazon basin was patchier than today (THOMPSON et al. 1995); and with reference to the low nitrate levels in the ice cores, the latter authors noted these "may imply that forest cover was significantly reduced in response to dry conditions and the expansion of grassland" (THOMPSON et al. 1995: 47). Additional geological and geomorphological evidence for dry climatic periods from Amazonia and other areas of tropical South America has been reviewed by several authors, for example, GARNER (1974, 1975), JOURNAUX (1975), BIGARELLA & FERREIRA (1985), AB'SÁBER & ABSY (1993), HOOGHMIEMSTRA & VAN DER HAMMEN (1998) and BEHLING (2001).

Only few of the above discussions of field data indicating fairly dry conditions in portions of Amazonia during certain geological periods have been taken into consideration by COLINVAUX et al. (2000) and COLINVAUX & DE OLIVEIRA (2000, 2001) who claimed that the forests of central Amazonia were never affected by dry climatic conditions and therefore were never fragmented by intermediate and fairly open vegetation (see also JONES 2001). On the other hand, VAN DER HAMMEN & HOOG-

MIEMSTRA (2000) reviewing the Late Tertiary and Quaternary history of vegetation and climate in Amazonia estimated that rainfall during the last glacial maximum may have been reduced by 30 -50 % leading to substantial shrinkage of wet rainforests and the formation of wet forest refuges separated by drier types of vegetation. Also, in none of the published records from Amazonia and central Brazil are sediments of the Last Glacial Maximum (LGM) present or abundant (LEDRU et al. 1998; VAN DER HAMMEN & HOOGHMIEMSTRA 2000 for Lake Pata). The LGM was represented by a hiatus of several thousand years or more, indicative of drier climates than before and after; "sediment changes attest to drier climates between ca 24,000 and 17,000 YBP" (LEDRU et al. 1998: 236). The climate of the High Andes of Bolivia and Peru was humid during the Last Glacial Maximum and, following this period, was characterized by a succession of very dry periods; BAKER et al. (2001) believe that these results also apply to much of the Amazon basin. On the other hand, paleoceanographer ALAN MIX thinks a high-pressure anomaly pushed rainfall out of the Amazon forest region, giving wet days in the Andes and drying out the Amazon lowlands; this explains the recent observations that water levels in Lake Titicaca rose during the glacial maximum (quoted in JONES 2001: 38). Similarly, HOSTETLER & MIX (1999) concluded that "seasonal drying in the OSU simulation extends well inland over the Amazon basin and Central America" during the Last Glacial Maximum; the Amazon lowlands were substantially drier than indicated by the earlier CLIMAP simulation. The results of the vegetation simulations for the Last Glacial Maximum by COWLING et al. (2001) are discussed below (under 'Canopy-density hypothesis'). The oxygen isotopic composition of planktonic foraminifera recovered from a marine sediment core in a region of Amazon River discharge shows that the Amazon Basin was extremely dry during the cool Younger Dryas period (ca 13,000 - 11,600 YBP), with the discharge reduced by at least 40 % as compared with that of today; effective moisture increased steadily afterwards during the Holocene (MASLIN & BURNS 2000).

BURNHAM & GRAHAM (1999: 569) concluded their excellent balanced review stating: "There are a number of indications that late Glacial and early Holocene climates in the neotropical lowlands included cooler and drier intervals, and variously supported a mosaic of moist forests and drier forests to savanna-like vegetation. These are: (1) fossil mammalian faunas in Central and South America [...]; (2) a trend toward drier conditions and a more complex array of communities developing near the end of the Tertiary Period in Costa Rica and Panamá [...]; (3) aridity at interglacial-glacial transitions in Guatemala [...]; (4) geomorphic features suggesting aridity during the Quaternary in the Amazon lowlands [...]; (5) marked changes in sea level [...]; and (6) Quaternary aridity demonstrated from other adjacent and distant parts of the world [...]"

"The combination of temperatures ca 6 °C cooler [during the LGM], sea level ca 120 m lower, and pollen sequences indicating at least locally dry habitats and open vegetation are compelling. They create a view of lowland neotropical vegetation alternating between closed forest and more dry open forest or savanna-like vegetation during the environmental fluctuations of the late Tertiary and Quaternary Period" (BURNHAM & GRAHAM 1999: 570):

The desiccation of tropical South America during dry climatic periods of the Cenozoic probably did not cause all of middle and lower Amazonia to become unforested and replaced by seasonally dry savanna and cerrado vegetation, as some recent authors illustrated in their schematic scenarios for the Pleistocene (e.g. CLAPPERTON 1993b; IRIONDO & LATRUBESSE 1994). Such a complete elimination of the rainforests would be unlikely for two reasons: firstly, what was the origin of the Amazonian rainforests that are now so widely distributed?, and secondly, how can the origin of the large number of allopatric species (and subspecies) in Amazonia be explained?

The ranges of many of these allopatric forms border each other along the opposite shores of the Amazon River and its major tributaries. It was therefore suggested that they had originated *in situ* during the Pleistocene or earlier geological periods with the rivers as barriers permitting the differentiation of these representatives (River theory or Riverine barrier theory). But this theory is contradicted in many areas by the following facts:

Rivers cease to form barriers in the forested headwater regions, where the representative populations are in direct contact (either hybridizing or excluding each other geographically without hybridization). As WALLACE (1852: 110) already stated: "On approaching the sources of the rivers they cease to be a boundary, and most of the species are found on both sides of them". This situation indicates a lack of geographical isolation in the headwater region between populations which indeed are effectively separated by the broad river courses further downstream. Direct application of the theory of allopatric speciation to such populations in contact in the headwater regions of Amazonian rivers is impossible.

Numerous Amazonian subspecies and species of rainforest birds and other animals abut along conspicuous secondary contact zones in continuous terra firme forest regions. Their locations, in many cases, are unrelated to large rivers which the contact zones cross at right angles (Fig. 2). Such areas of contact represent major zones of biogeographic discontinuity in a continuous forest environment (HAFFER 1997a, 2000).

Several representative taxa inhabiting the forest interior, whose ranges are separated by river courses, occupy (as uniform and phenotypically undifferentiated populations) extensive areas which are traversed by larger rivers than those that separate the respective ranges of these representatives. Future analyses will demonstrate whether or not such phenotypically uniform populations exhibit strong genetic differences.

(1) Genetic population studies of Amazonian rats (DA SILVA & PATTON 1993), frogs (GASCON et al. 1998) and Saddle-back Tamarins (PATTON et al. 2000) revealed spatial patterns in the Rio Juruá region that do not support the river theory but are more consistent with an interpretation of populations having established secondary contact in this region. As discussed by PATTON et al. (2000) and other authors, the phylogeographic relations of taxa inhabiting opposite river banks permit a distinction to be made whether these taxa are in secondary or primary contact or whether dispersal from one side of a river to the opposite bank has occurred. The examples mentioned above favor an interpretation of secondary contact (situation B in Fig. 3) implying large-scale separation of the respective populations during one or more periods during the geological past (either through vegetational changes or through geological-geomorphological changes in the landscape).

(2) The river theory is also in conflict with the geological record because many of the allopatric species now occur in areas that were presumably fairly dry and unforested or only lightly forested during certain climatic periods of the past.

However, the Riverine Barrier Model seems to be applicable to an interpretation of subspeciation and perhaps also speciation in the *Callithrix* marmosets (ROOSMALEN et al. 2000) and possibly in some birds (HAFFER 1992) of the Rio Madeira-Tapajós-Xingú region in southeastern Amazonia. The rather straight rivers and their tributaries in this area flow down the relatively "steep" northern slope of the Brazilian Shield which precludes meandering and, with it, passive cross-river transport of sedentary animal populations through cut-off of meander loops. The populations of the *Callithrix* marmosets in the various interfluvia are well differentiated in pelage color. However, it remains unknown which of these conspicuously different forms intergrade in the headwater regions (subspecies) and which overlap their ranges without hybridization (species).

The refuge theory (HAFFER 1969, 1974, 1982; VANZOLINI & WILLIAMS 1970; VUILLEUMIER 1971; VANZOLINI 1973; MÜLLER 1973; PRANCE 1973, 1982a; BROWN et al. 1974; SIMPSON & HAFFER 1978; BROWN & AB'SÁBER 1979) was proposed as an alternative to the Riverine Barrier hypothesis and it postulates the persistence of extensive 'patches' of wet rainforests especially in those portions of the Amazonian lowlands where enough surface relief was present to create rainfall gradients during generally dry phases of the Cenozoic (Tertiary and Quaternary), e.g. near the Andes, along the slopes of many mountains of southern Venezuela and of the Guianas, as well as to the north of the Parecí mountains in central Brazil and near the Atlantic Ocean in eastern Pará. It is probable that the size of these patches of wet forest during the dry periods was larger and much less well defined than what has been shown on many maps illustrating the location of Amazonian rainforest refugia. Central to the Refuge model is the postulated fragmentation of the Amazon rainforest into a number of wet forest blocks, not the larger or smaller size of these rainforest patches during the peaks of various dry climatic phases. The wet forest 'refugia' are assumed to have been separated by various types of savanna, dry forest, liana forest and other intermediate vegetation types of seasonally dry climates which would have been effective barriers to the dispersal of wet rainforest plants and animals. Under this model, refugia represent relatively stable areas through time, located in peripheral portions of Amazonia, from where the recolonisation of the lowlands in central Amazonia took place upon the return of humid climatic conditions. Here species 'accumulated' spreading from adjacent 'ecotonal areas' of the region. The Refuge theory remains a working model because the geological-palynological data from Amazonia are still insufficient to prove the fragmentation of the wet rainforest region by intermediate and dry vegetation types during particular dry periods (which may or may not coincide with the coldest climatic phases).

The first proof for the continued existence of moist forests in one particular region during the last glacial maximum was recently furnished by COLINVAUX et al. (1996) in a long pollen record from an area in northern Brazil which was one of the original forest refugia proposed by HAFFER (1969; Imerí refugium). The sediment core from which these pollen spectra were extracted was taken from the bottom of Lake Pata (Fig. 1) located only 60 kilometers southwest of the Neblina-Imerí mountain range which rises to 3000 meters elevation in the border region between Venezuela and Brazil. The Lake Pata pollen record of the last glacial maximum indicates, for that period, the

existence in this region of tropical rainforest which, however, also included some plant taxa which are presently confined to lower montane levels. The Lake Pata record established the fact that, in the lowlands surrounding the Sierra Neblina-Imeri, tropical rainforest indeed existed during the generally dry last glacial phase (as had been predicted by the refuge theory; Lake Pata is located in the southern peripheral portion of the stippled area outlining the Imeri Refugium in Figure 5 of HAFFER [1969] and which, of course, might have been more extensive than schematically indicated in that sketch). HOOGHMSTRA & VAN DER HAMMEN (1998: 157), BURNHAM & GRAHAM (1999: 568) and VAN DER HAMMEN & HOOGHMSTRA (2000) also pointed out that Lake Pata is located in an area that had previously been predicted as having been humid during the generally dry Last Glacial Maximum (see VAN DER HAMMEN & ABSY 1994). The Lake Pata record, valuable as this field data is, cannot be used as a criterion to distinguish between the refuge theory and the disturbance-vicariance theory, as was done by COLINVAUX et al. (1996, 2000) and COLINVAUX & DE OLIVEIRA (2000, 2001).

In Ecuador, fossil pollen data are available only from the eastern slopes of the Andes at ca 1100 m elevation, i.e. above the Amazonian lowlands, indicating that, during the last glacial period, moist forests with Andean elements existed in this region (COLINVAUX 1993, COLINVAUX et al. 1997; see also comments by HEINE 1994). These Andean sites are located ca. 500 m higher than (not within) the putative Napo forest refuge of the Amazonian lowlands of Ecuador near the base of the mountains. Future palynological studies will probably prove the existence of closed rainforest during generally dry climatic phases of the Pleistocene also in other portions of Amazonia, e.g. near the Andes of southeastern Peru, in southcentral Amazonia and to the south of the mouth of the Amazon River. These Pleistocene forests were 'tropical' in the sense that they were inhabitable for tropical lowland faunas, although the plant species composition may have changed to some extent.

The refuge theory proposes that vegetational changes following climatic reversals due to Milankovitch cycles *during any period of the earth's history* caused the fragmentation of species ranges and the isolation of a portion of the respective biotas into ecological refuges, where species populations (1) became extinct, (2) survived unchanged, or (3) differentiated to the level of subspecies or species (in accordance with the theory of geographic speciation, MAYR 1942, 1963). Newly differentiated species probably survived many periods of environmental change before they speciated again. We emphasize that the theory is not restricted to the Pleistocene, but applies also to biotic differentiation during the Tertiary and earlier when, as during the Quaternary, Milankovitch cycles caused sea-level oscillations, rhythmic facies changes of geological strata, and climatic-vegetational changes on the continents (HERBERT & FISCHER 1986; OLSEN 1986; BARTLEIN & PRENTICE 1989; BERGER et al. 1989; ZACHOS et al. 1997, 2001; BENNETT 1997). There is evidence that many extant species had already become isolated during the Pliocene, when they may have originated in Tertiary forest refugia. Refuge theory refers to the postulated origin of species and subspecies in ecological refugia (forest and nonforest) on the continents irrespective of the time periods, i.e. during the entire Cenozoic and before (HAFFER 1993).

Following BENNETT (1997: 185) it is reasonable to consider events during the Quaternary as representative of the 20,000 to 100,000 year time-scales throughout earth history. Disruptions of communities and speciation in geographically isolated popula-

tions created by perpetual environmental changes of Milankovitch time scales has been a permanent feature, although usually unrecognized because of the relatively coarse resolution of most of the geological and paleontological record.

Cautions with the application of refuge theory that need to be taken into consideration include: (1) Gallery forests promote gene flow between refugia and probably reduction of the amount of differentiation; (2) only ecologically narrowly adapted forest species were affected, whereas populations of ecologically more flexible species are unlikely to have been isolated effectively in refugia.

Biogeographic evidence supporting the refuge theory include the coincidence of areas of endemism in different groups of organisms (Fig. 4) and the occurrence of sharply defined contact zones between certain subspecies and species of Amazonian forest birds which represent zones of conspicuous biogeographic discontinuity in a continuous forest environment (Fig. 2). RON (2000) and BATES (2001) studied the areas of endemism of different vertebrate groups cladistically using Parsimony Analysis of Endemism to produce hypotheses of area relationships. The three main clusters are (1) Belém, (2) Guiana and (3) Upper Amazonia (Napo + Inambari). In the case of hybrid zones between subspecies, these zones have two characteristics which one would expect to find in zones where populations established secondary contact after a period of separation: (1) populations in the hybrid zone have greatly increased variability; and (2) outside the hybrid zone, the two forms are, over wide areas, relatively uniform, at most varying gradually (clinally) over great distances. Additional evidence is provided by taxa of forest birds that are restricted to one or two localized forest regions in Amazonia, but absent elsewhere, and taxa with disjunct distribution (HAFFER 1974, 1997b; MAYR & O'HARA 1986). Several other authors observed similar biogeographical phenomena and interpreted them in a corresponding manner for plants (PRANCE 1973, 1982a, 1987, 1996), reptiles (VANZOLINI & WILLIAMS 1970; VANZOLINI 1992), fishes (HUBER 1998), butterflies (BROWN 1976, 1987b; BROWER 1996), and mammals (CERQUEIRA 1982). We may also mention the close relations between certain nonforest faunal and floral elements of the areas to the north and south of Amazonia and which require temporary connections across these forested lowlands.

Misconceptions of the Refuge theory: Several misconceptions in the recent literature regarding the Refuge Model for Amazonia include the following (references in HAFFER 1993):

(1) The Refuge model supposedly was based only on present biotic patterns. Actually, it was developed by combining data sets from two independent sources. One set of data involves information from paleobotany, geomorphology, and climatic extrapolations. The second comes from analyses of modern plant and animal distribution patterns. From each independently derived set, predictions could be made about the distribution of lowland forest during dry climatic phases of the Pleistocene. The coincidence between the location of presumed forest refugia derived from these two independent sets of data led to the formulation of the general theory (SIMPSON & HAFFER 1978);

(2) The Refuge model supposedly refers to a single Late Pleistocene vicariance event. Actually, a series of climatic-vegetational reversals and associated vicariance events during the course of the entire Quaternary were hypothesized to have caused biotic differentiation (HAFFER 1969; "Within the last two million years the forest appears to have undergone repeated episodes of shrinkage and expansion", SIMPSON & HAFFER 1978: 513).

(3) The Refuge model supposedly applies only to the Pleistocene. Actually, the theory refers also to the Tertiary and earlier periods (HAFFER 1993 and see above).

(4) All evolution of the Neotropical biota supposedly took place in Quaternary refugia and all extant species are Quaternary in age. No author ever made such claims.

(5) The regions between the postulated wet forest refugia supposedly were covered exclusively by grass savannas. Actually, it was speculated that "There were probably additional smaller forests along the major river courses of Amazonia, on the slopes of isolated mountains, and in the extensive lowlands between the upper Rio Madeira and the Marañón River" (HAFFER 1969: 134). "Vegetation types, such as dry forest, transition forest, liana forest, and bamboo forest, would break up the distribution of many species and would be equally effective as a cause of vicariance" as savanna or cerrado (PRANCE 1981: 400). "Between the isolated humid areas where rain forest persisted would have lain a complex mosaic of the different vegetation types of seasonally dry climates which would have been an effective barrier to the dispersal of most rain forest plants and animals" (BROWN 1987a: 43).

(6) Each period of refuge formation supposedly always led to full speciation in the separated populations. Actually, this is rather unlikely and has never been suggested by any author.

(7) All newly differentiated species supposedly spread out widely from the areas of the former refugia when humid conditions had returned. Actually, many endemic species have very restricted distributions today.

(8) During glacial times, supposedly no lowland forest refugia existed in Middle America which region was recolonized by postglacial forest expansion from distant South American refugia. No author ever made such claims. Actually, the probable existence of a series of Pleistocene forest refugia in the Pacific and Caribbean lowlands near the Middle American mountain ranges has been discussed for over 30 years.

The above list indicates that many "straw-men" have been used to criticize the refuge theory in the recent literature.

History of the Refuge theory: The theory of speciation in ecological refugia was originally developed by Edward FORBES in 1846 (as mentioned by MAYR & O'HARA 1986) and was later applied by STRESEMANN (1919), STRESEMANN & GROTE (1929) and several other authors of the 1930s who studied the origin of closely related members of avian species pairs of the north Temperate Zone and in tropical Africa. Authors of general zoogeographical works indicated the importance of the repeated appearance and disappearance of vegetational barriers for the speciation process and ensuing adaptive radiation in many groups of tropical and high latitude organisms (MAYR 1942, 1963: 561; DARLINGTON 1957). The theory was subsequently applied to the avifaunas of Australia (KEAST 1961; JOSEPH et al. 1995; WILLIAMS & PEARSON 1997; SCHNEIDER et al. 1998), tropical Africa (MOREAU 1966; CROWE & CROWE 1982; VRBA 1995; LÉVÊQUE 1997), the Neotropical region (HAFFER 1969, 1974; VANZOLINI & WILLIAMS 1970; VUILLEUMIER 1971, VANZOLINI 1973; PRANCE 1973; MÜLLER 1973; PRANCE 1982a, b), the Malay Archipelago (BRANDON-JONES 1996, 1998 [primates]) and New Guinea (PRATT 1982, BEEHLER et al. 1986: 21). Modern phylogeographic studies have confirmed this dynamic view of global biogeography during the last several million years (HEWITT 2000; AVISE 2000). The Refuge Model for Amazonia (and other tropical regions of the world) remains a viable working hypothesis until tests will be possible when additional

palynological, geological and geomorphological data become available from this region during the course of the next several decades, in particular from *terra firme* regions in central Amazonia between and at a distance from large rivers.

Alternative allopatric speciation models

Canopy-density hypothesis: Recent modeling research investigated possible responses of vegetation in the Amazonian lowlands to the climate of the last glacial maximum (LGM), focusing on the balance between changes in vegetation type and structure (COWLING et al. 2001). Most of the simulated 20 % decrease in forest cover during the LGM occurred near the southern margins of the basin and several localized regions of xeric vegetation types were introduced within central Amazonia. The results also suggest repeated reductions and increases in forest canopy density over large areas during glacial-interglacial cycles. Alterations in the canopy microclimate were probably brought about by glacial cooling, aridity, and low concentrations of CO₂ leading to individualistic changes in the distribution of plant and animal species. During glacial periods, forests with reduced canopy humidity and relatively high temperatures probably had a wider distribution than today which probably led to interruption of gene flow (vicariance) in many species and subsequently to speciation. Under this hypothesis, biological separation of gene pools does not necessarily require forest fragmentation but only a change from wet to dry forests.

The canopy-density hypothesis applies not only to the Pleistocene but also to much earlier periods in the Cenozoic, because forests are independently (and interactively) influenced by decreases in temperature, precipitation, and atmospheric CO₂. Paleoclimate reconstructions indicate that relatively low CO₂ and high temperatures could have resulted in large spatial variations in forest vegetation, thereby geographically isolating species over time.

This theory is not very different from the Refuge hypothesis. Both models propose that large-scale vegetation changes occurred in Amazonia during periods of climatic changes (precipitation, temperature, CO₂) leading to an expansion of dry-adapted forest and nonforest vegetation. Both models refer not only to the Pleistocene but also to older geological periods. Based on geomorphological field data from central Amazonia and the wide distribution of savanna plants, the Refuge hypothesis emphasizes a rather widespread occurrence of open vegetation in Amazonia during dry climatic periods, whereas the simulations of COWLING et al. (2001: 142) introduced only "a few localized regions of xeric vegetation types" within central Amazonia. However, in view of the fact that, under the Refuge hypothesis, not only open vegetation zones but also regions covered with various types of dry forest and other intermediate vegetation types acted as barriers for wet rainforest animals, both hypotheses have more similarities than differences.

COLINVAUX (1998) presented another vicariance model of speciation in Amazonia, the '*disturbance-vicariance*' hypothesis. He believes that, during glacial periods of the Pleistocene, the slightly elevated sites of the postulated forest refugia in peripheral regions of Amazonia actually represented cool, CO₂ deficient 'islands' in a 'sea' of continuous tropical lowland forest (rather than wet forest 'islands' in a 'sea' of fairly open and intermediate vegetation types). The following considerations argue against this

hypothesis: (1) It is unlikely that the elevational difference of 100 to 200 meters between the bottomlands and the peripheral refuge areas (and associated differences in average temperature and CO₂ content) had such a massive effect on the biota as claimed; (2) The numerous paleoecological records from many regions in Amazonia discussed above and the present day distribution of many savanna plant species, indicate widespread dry climatic conditions during several periods of the Pleistocene. Except for the very few palynological records little of this information has been taken into consideration by COLINVAUX; (3) This vicariance model applies only to the alternating cold/warm climatic periods of the Pleistocene but leaves unexplained the mechanism of speciation in Amazonia and other regions of the tropics during the much longer and generally warm Tertiary period, when very active biotic differentiation took place (and most extant species originated) probably due to the effect of humid and dry climatic phases caused by pre-Quaternary Milankovitch cycles. Thus the refuge theory (applying to the entire Cenozoic) and the disturbance-vicariance theory (applying to the Quaternary only) are not alternatives.

BUSH (1994) also stated that climatic cooling, rather than dryness, was the factor driving a Pleistocene re-assortment of vegetation in Amazonia. However, he did accept climatic drying (by about 20%) over Amazonia during glacial periods, which led to expansion of dry-adapted vegetation types into the transverse climatic belts crossing lower (central) Amazonia from southeast to northwest and also crossing southwestern Amazonia along the border region of Peru and Brazil (his Fig. 3). In this way he accepted a separation of humid rainforest blocks in the Guianas and at the mouth of the Amazon River from the upper Amazonian forests as well as a separation of lowland forests ('refugia') along the base of the Peruvian Andes from the extensive forests of upper Amazonia. Apparently BUSH had species-specific refugia in mind when he stated: "If the cooling and drying stressed individual species to the point where they went extinct over parts of their range and only survived in areas that were optimal, a mechanism for allopatric speciation emerges". This is an extension of COLINVAUX's disturbance-vicariance hypothesis' which is based on the premise that the forest of central Amazonia was probably not markedly fragmented (COLINVAUX 1993, 1996). Both COLINVAUX (l.c.) and BUSH (l.c.) suggested that areas of highest species endemism in peripheral regions of Amazonia are regions of maximum disturbance (rather than maximum forest stability in forest refuges); this assumption is unlikely and requires re-examination (MORLEY 2000: 129, 279).

COLINVAUX et al. (2000) reviewed the palynological record at three data points in Amazonia and one sample location offshore concluding that no portion of Amazonia ever experienced comparatively dry climates during certain periods of the Quaternary. Their data base from this vast region is clearly insufficient to arrive at such a sweeping conclusion. Moreover these authors did not take into consideration many geomorphological data indicating dry climates and open vegetation as reviewed above, nor the distribution of savanna plant species. Regarding the results of pollen analyses of marine sediment cores from off the mouth of the Amazon River (HABERLE & MASLIN 1999), there are several reasons to doubt the value of the pollen signal, as discussed by HOOGHMSTRA & VAN DER HAMMEN (1998): (1) graminaceous pollen grains may be derived from savanna-like vegetation or from floating grass-rich meadows; (2) mixing and redeposition of sediments during glacial sea-level stands that were up to 120 m lower than today; (3) large gallery forests along the river courses in Amazonia

probably prevented pollen grains from savanna vegetation to reach the river system. Savanna vegetation is expected to be poorly represented in the river-transported pollen spectrum. According to HOOGHMSTRA & VAN DER HAMMEN (1998) and VAN DER HAMMEN & HOOGHMSTRA (2000) the conclusions of COLINVAUX et al. (1996, 2000) with respect to a stable rainforest cover of Amazonia since the last interglacial period are unjustified.

Museum hypothesis: FJELDSÅ et al. (1999: 63, 76) associated the origin of new species with very restricted and ecologically extremely stable areas in the foothills of the mountainous regions around Amazonia from where new species supposedly spread into the bottomlands and here 'accumulated' over time. The latter authors are of the opinion that "speciation in forest birds may not necessarily require the development of large 'barriers' of non-forest habitat (as assumed by the refuge theory). A specialised bird could also vanish over large areas because of increased species turnover resulting from high functional heterogeneity of habitats". Such models, even if feasible from a theoretical point of view, are contradicted by the geoscientific evidence for widespread vegetational changes over Amazonia during alternating dry and humid climatic periods of the Quaternary and probably during earlier periods as well.

Paleogeography hypothesis: The comparatively simple paleogeographical setting of the Amazon basin between the Guiana shield to the north and the Brazilian shield to the south, during the Tertiary period (of 60 million years duration), does not seem to provide a sufficiently complex and rather rapidly changing geological theater to have caused the intensive evolution, ecological differentiation and speciation in the lowland floras and faunas that certainly took place there during those times. This paleogeographic situation as discussed and illustrated by HARRINGTON (1962) and PETRI & FÚLFARO (1983) may have provided no more than the basic framework for evolution to proceed. It appears likely that climatic-vegetational fluctuations caused by Milankovitch cycles, led to frequent ecological vicariance through vegetational changes on these land regions (Guiana shield, Brazilian shield, foothills of the growing Andes mountains) causing more pronounced speciation and evolution than through the paleogeographical changes in the distributions of land and sea. In recent years, many cladograms have been published for the species of genera and families of South American animals and plants illustrating numerous splits of evolutionary lineages during the course of the Tertiary usually with no discussions of the probable nature of the vicariance events underlying such cladogenetic events (which in many cases may have been caused by ecological vicariance). NORES (1999) and BATES (2001) are of the opinion that the paleogeographical development of the greater Amazon region included sufficient vicariance events to explain the complex differentiation of the neotropical fauna (basically with no additional mechanisms for vicariance of populations required). Thus these authors related the origin of extant species and subspecies of birds to the separation of the Andean forelands, the Guiana shield and the Brazilian shield by marine incursions ca 2 - 4 million years ago ('Island' hypothesis). It should be noted that the uplift of the Andes mountains in Oligocene and Miocene times created an important barrier between the trans- and cis-Andean lowlands, although many Amazonian elements were able to invade the Pacific Colombian and Middle American rainforests via the northern Colombian lowlands during later geological periods.

Additional allopatric speciation models that have been proposed for Amazonia in recent years include the 'River-refuge' hypothesis, the 'Lake' hypothesis, and the

'Arch' hypothesis. However, little geological support can be adduced for any of these models. According to the *River-refuge hypothesis*, plant and animal populations presumably have been isolated by a combination of the broad lower courses of Amazonian rivers and extensive unforested or poorly forested terrain in the headwater regions of northern and southern Amazonia during dry climatic periods, when the zone of tropical forests supposedly contracted toward the equator on broad latitudinal fronts, leaving central Amazonia unaffected (AYRES & CLUTTON-BROCK 1992). However, probably also portions of central Amazonia were influenced by climatic fluctuations. The *Lake hypothesis* is based on the assumption that most of Amazonia was covered by a huge lake or lagoon at the end of the Tertiary (Pliocene) and successively smaller portions of Amazonia were covered during a series of assumed high sea-level stands during the Quaternary, as supposedly documented by corresponding terrace levels in the lower Amazon Valley (KLAMMER 1984; MARROIG & CERQUEIRA 1997). Proponents of this model assume that the flooding pushed the rainforests to peripheral regions of the Amazon basin where, in addition, the broadened rivers separated populations of animals and plants on forest 'islands'. However, the terrace levels in lower Amazonia probably have been uplifted tectonically to their present elevation and are not due to high water levels in Amazonia (CLAPPERTON 1993b: 59).

The *Arch hypothesis* proposes that certain (unknown) surface expressions of several tectonic cross elements or 'arches' at depth (subdividing the Amazon basin into a number of geological sub-basins) separated the ranges of plant and animal species thus permitting their differentiation (PATTON et al. 1997, 1998, 2000). We emphasize that the results of the latter authors from the Rio Juruá region in southwestern Amazonia disprove only the predictions of the Riverine barrier hypothesis and are more consistent with an interpretation of populations in secondary contact in this region today (see above). Secondary contact may be explained either on the basis of the Refuge hypothesis or the Arch hypothesis (of which PATTON et al. preferred the latter). The Iquitos arch discussed by these authors originated through tectonic movements during the Jurassic period. Unlike the geological arches in the immediate Andean forelands, this arch was hardly active during the deposition of the Cretaceous and Tertiary formations (see further discussion in HAFFER 1997b). It still remains unknown whether the position of contact zones between small mammals of the Juruá region follows the N-S extension of the Iquitos arch at depth, as assumed by PATTON et al. (2000) or some other direction. The contact zones between members of several pairs of representative taxa of birds found in this same general region of the upper Rio Juruá (e.g. *Neomorphus geoffroyi*/*N. pucheranii* and *Pipra fasciicauda*/*P. filicauda*) extend in an east-west direction (Fig. 2), i.e. more or less perpendicular to the position of the Iquitos arch at depth (with which the origin of these taxa and their contact zones very probably have nothing to do).

We emphasize that the various hypotheses mentioned above have very different significance (explanatory powers) as speciation models for Amazonia. The explanatory power is high in the cases of the paleogeography hypothesis, the refuge hypothesis, and the canopy-density hypothesis, because they refer to a long time span (Tertiary and Quaternary and before) and to recurrent events of barrier formation (repeated changes in the distribution of land and sea and of wet and dry vegetation types on land areas). The explanatory power is low in the case of those hypotheses which either refer to unique historical events (e.g. the origin of the Amazonian river system) or to a short

geological time span, e.g. the Pleistocene only, after many or most extant species had originated (as in the case of the disturbance-vicariance hypothesis).

Conclusion

It appears likely that in Amazonia and in other tropical regions of the world, the distribution and species composition of wet and dry forest as well as nonforest biomes changed continuously during the Cenozoic and earlier. The wet forest was broken up into isolated blocks that later coalesced under varying climatic conditions. Due to the effect of Milankovitch cycles, wet forest and nonforest refugia probably formed during the peaks of (cool-)dry and (warm-)humid climatic phases leading to 'turn-over pulses' in the evolution of floras and faunas during the Quaternary-Tertiary and earlier periods (VRBA 1992, 1993).

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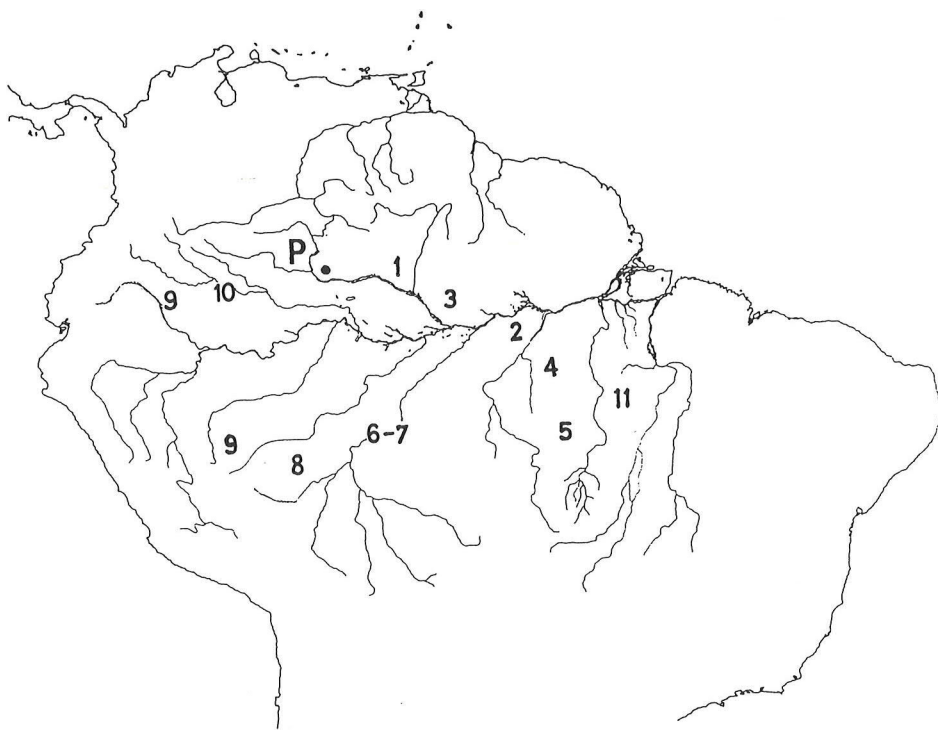


Fig. 1:
Location map of areas in Amazonia where paleoecological evidence for dry climatic periods and associated vegetational changes of the late Pleistocene has been gathered in recent years (see text for explanation of the numbers). A rich data base for climatic-vegetational shifts during the Quaternary is available from northern South America and central Brazil outside Amazonia (not indicated on this map). **P** (black dot) - location of Lake Pata.

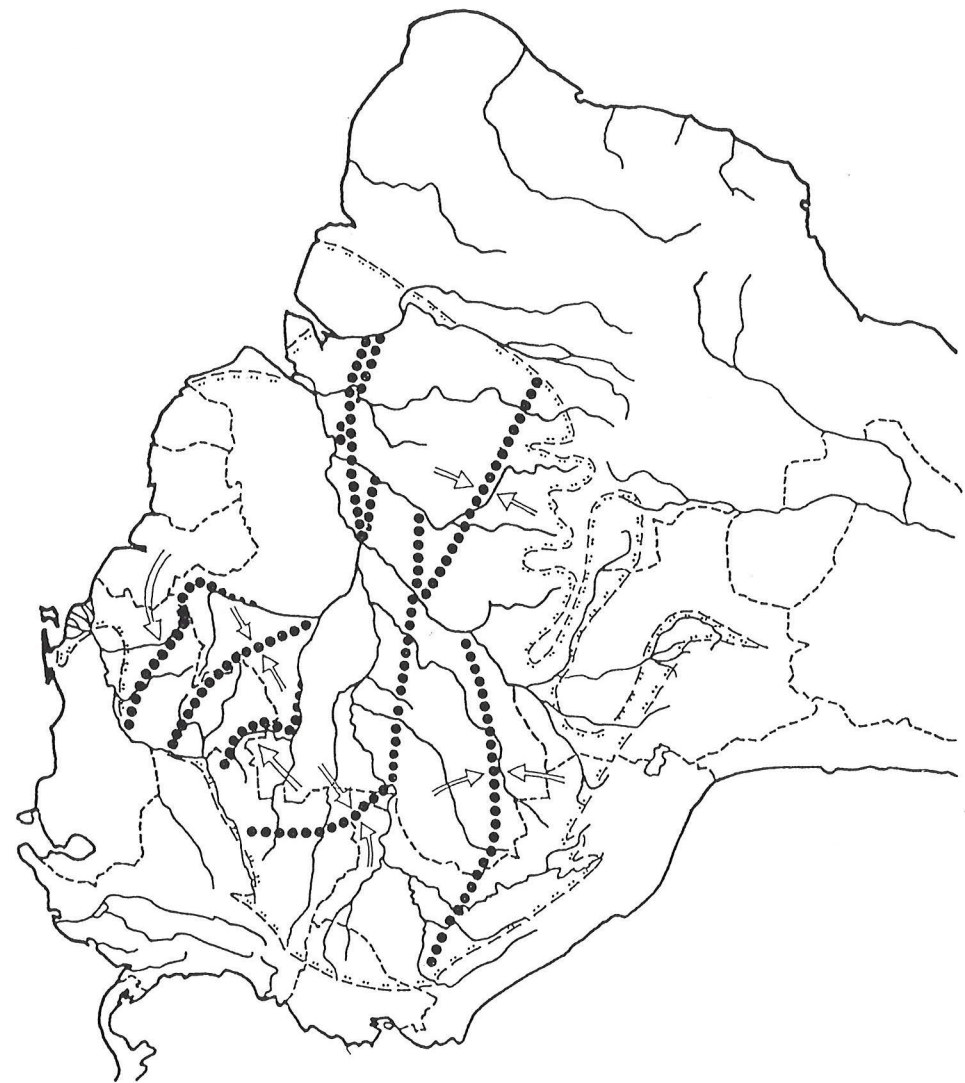


Fig. 2:
Contact zones between taxa of selected Amazonian birds whose locations are independent of or variously displaced by river courses. Other contact zones follow the Amazon River and the lower portions of most major tributaries (from HAFFER 1997a, 2000).

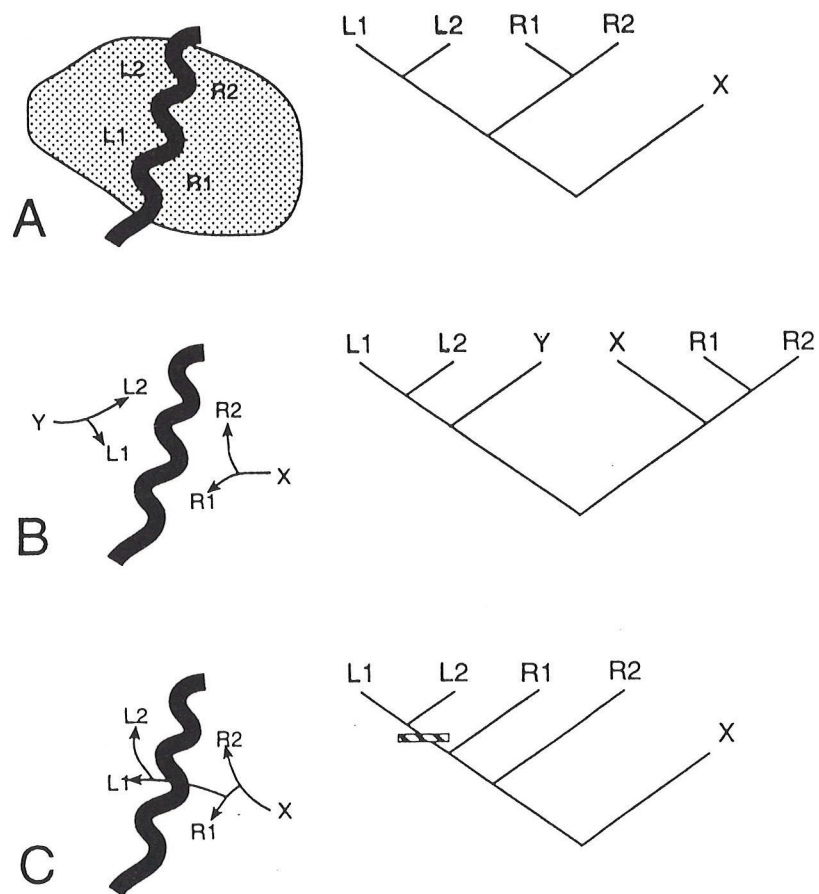


Fig. 3:

Three alternative phylogeographic hypotheses. **A:** Primary diversification: reciprocally monophyletic and sister clades bounded by a river that imposed itself on an existing species range. **B:** Secondary contact: reciprocally monophyletic, but nonsister clades, bounded by a river that served as the secondary meeting point of clades that evolved elsewhere. **C:** Dispersal: paraphyletic relationship of right bank haplotypes relative to left bank ones due to one episode of cross-river transfer. From PATTON et al. (2000).

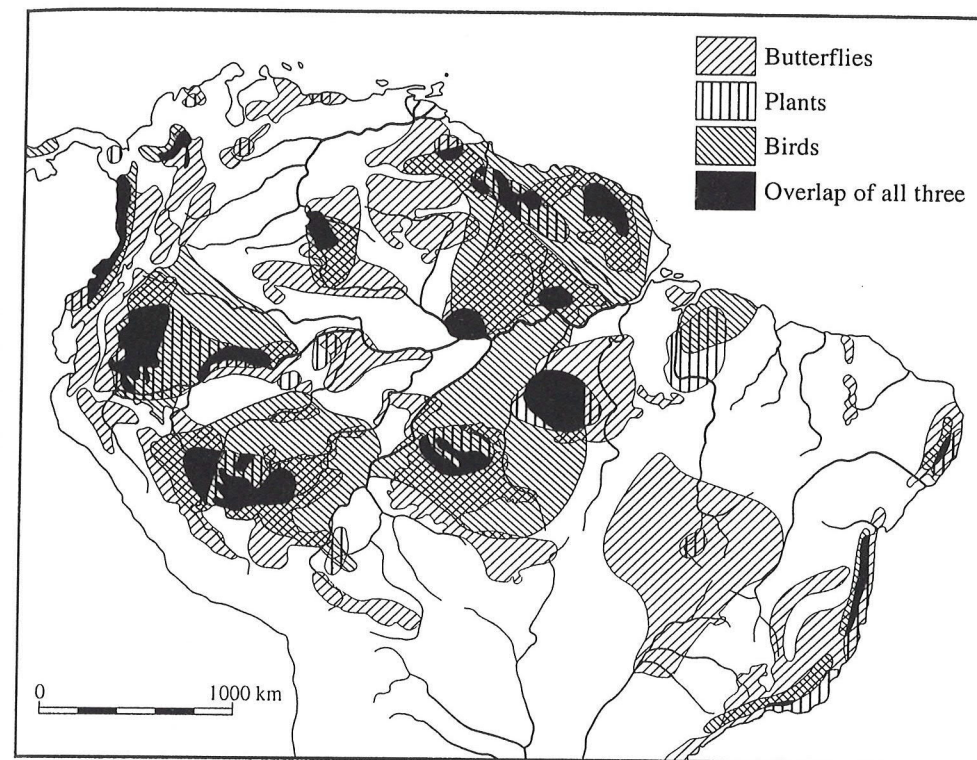


Fig. 4:

Superimposition of endemism patterns in Neotropical plants, butterflies, and birds. Adapted from BROWN (1987c).

Addendum

In the above article, we based our discussions of the climatic-vegetational history of Amazonia on the field data and interpretations of specialists in various fields of the earth sciences indicating the effect of variously dry climatic phases in portions of Amazonia during different geological periods. These specialists are the palynologists T. VAN DER HAMMEN, H. HOOGHIEMSTRA, M. ABSY, the geomorphologists A.N. AB'SÁBER, E. BIBUS, J.J. BIGARELLA, A. JOURNAUX, M. IRIONDO, J.S. BETTENCOURT, B.I. KRONBERG, E.M. LATRUBESSE, M.-P. LEDRU, J. BERTAUX, J.O.S. SANTOS, K. SUGUIO, J. TRICART, A.T.C. VEIGA as well as the paleontologists A. RANCY and S.D. WEBB.

In their critical comments on the refuge theory, COLINVAUX et al. (2001) claim that the interpretations of all of the scientists mentioned above are spurious because they supposedly distorted and routinely misinterpreted their field data in favor of the preconceived idea of ice age dryness. Certainly, these rather simplistic claims will lead to intensive discussions among earth scientists in future years.

According to COLINVAUX et al. (l.c.), wet tropical climates with humid weathering have prevailed in Amazonia since at least the Miocene with no dry phases interrupting the continuously humid climatic history of this region (except for minor vegetational fluctuations in peripheral portions of Amazonia). These authors did not specifically comment on the field data of BIBUS (1983), VEIGA (1991) and VEIGA et al. (1988) which carry particular weight in our interpretations. BIBUS (l.c.) described complex soil profiles and the widespread occurrence of coarse debris in southcentral Amazonia and pointed out the existence of thick layers of coarse sediments in the Pleistocene terraces found in lower Amazonia (and whose origin requires an explanation). He studied the road cuts along the Transamazonica south of Santarém and, among other phenomena (see our text above), described a "stone line consisting of coarse angular pieces of quartz. Form and texture of these quartz pieces indicate that they did not originate through secondary silica precipitation but no doubt are residual gravel derived from quartz veins within the [outcropping] granite. Therefore this stone line can be taken unequivocally as proof for an earlier erosional phase" in this region (BIBUS, l.c., p. 83). We mention this observation here as a reminder that, besides the "pseudo stone lines" consisting of concretions (discussed at length by COLINVAUX et al., l.c.), true stone lines also exist in Amazonia. VEIGA et al. (l.c.) described coarse and poorly sorted sediments underlying rainforest vegetation to the north of Manaus and in the Tapajós and Xingú River basins and discussed the paleoecological implications of these deposits. Obviously, additional field studies in these regions are highly desirable.

The statements of COLINVAUX et al. (2001) illustrate two of the misconceptions of the refuge theory that we mentioned in our text: (1) The proposal of the model over 30 years ago supposedly was based exclusively on present biotic patterns, when in fact also the results of previously published geomorphological and palynological studies have been used; (2) vegetational changes having taken place in Amazonia supposedly alternated between rainforest and grass savanna, when in fact much more complex changes from humid forest to dry forest, liana forest, bamboo forest and other vegetation types of seasonally dry climates have been envisaged.

Concluding this brief addendum we would like to point out that, contrary to the claim of COLINVAUX et al. (l.c.), we did not attempt to discredit all of the alternative

speciation models proposed for Amazonia, but instead stated that some aspects of most of them may be applicable to certain periods in the evolution of the biota. We emphasized, however, the very different significance (explanatory power) of the various alternative models depending on whether they refer to a long time span and recurrent events of barrier formation (highly significant) or to a short geological period and unique historical events (low significance).

COLINVAUX, P.A., IRION, G., RÄSÄNEN, M.E., BUSH, M.B. & J.A.S. NUNES DE MELLO (2001): A paradigm to be discarded: Geological and paleoecological data falsify the HAFFER & PRANCE refuge hypothesis of Amazonian speciation. - *Amazoniana* 16(3/4): 609-646.